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LIGHT AS A FACTOR IN CONTROLLING THE START OF DAILY ACTIVITY OF A WREN AND STINGLESS BEES

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Allard (1930, American Naturalist, LXIV) discussed the relation between the times at which various birds start their singing and the time of sunrise. It seems quite evident from the data which he gave that there is a relation and that light is probably the controlling factor.

At Barro Colorado, Canal Zone, I observed a wren (*Troglodytes musculus*) which spent its nights under the northeast corner of the roof of the laboratory of the Institute for Tropical Research. On twenty-four mornings between November 9 and December 5, 1930, the times at which this individual wren first sang fell within a range of fifteen minutes.

In the absence of a standard chronometer, the following device was used for assuring comparable time-readings. A narrow slit was sawed in a board which was about an inch thick. This board was then fastened about six inches above another, each being horizontal and the slit approximately in a north-south direction. The sun, when at the zenith, shone through this slit onto the lower board on which a mark was made to indicate the position of the light-streak at approximate noon. Whether this was exactly astronomical noon or not, it served to keep the daily readings to a standard.

Light was measured with a General Electric foot-candle meter recalibrated just before starting the series of observations. The instrument was held at the same place for each reading. This place was about twenty-five feet from the wren's retreat, with the instrument facing the zenith but receiving full eastern light. Naturally, the units read were not those of the light where the bird was but the two sets were probably closely correlated.

The problem is, essentially, whether this bird was a photometer, an alarm clock, both, or neither.

Sunrise at that latitude (9° N.) occurred at 6:11 on November 9 and at 6:15 on December 5, but the light-changes caused by this difference in time of sunrise were combined with and largely masked by differences in cloudiness as the season changed from the rainy to the dry. Figure 1 shows the recorded light at various times, each small circle

representing the average of all readings for a given three-minute interval. The curve was drawn by inspection to fit these averages. The times of the first morning song are represented by small S's. Although varying cloudiness noticeably affected the light, weather conditions were rather constant and between 5:45 and 6:05 light was fairly definitely correlated with time, making it difficult to determine whether the starting of song is a function of time or of light.

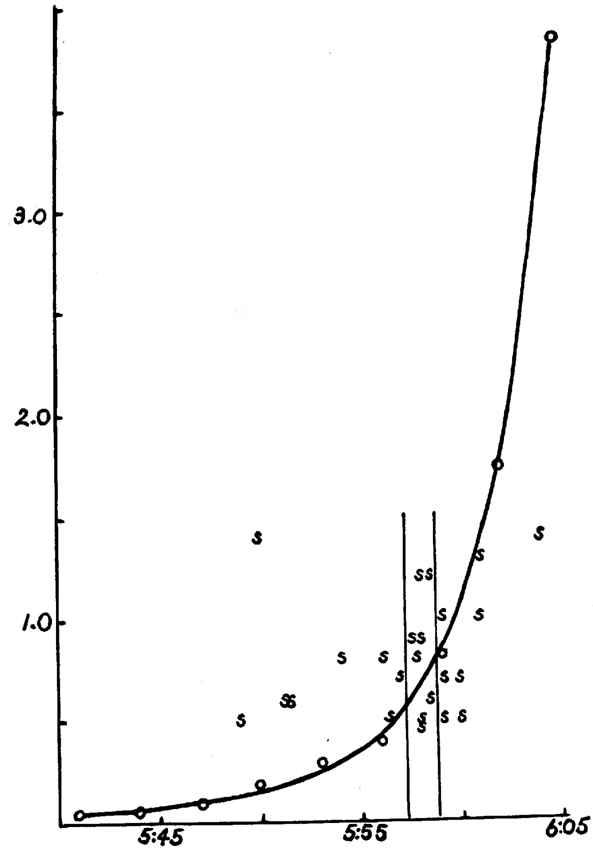

Fig. 1.—See text.

On eight of the twenty-four mornings for which observations were made the first song came between 5:57½ and 5:58½. The light at the times of these songs varied from 0.5 to 1.2 foot-candles, the average being 0.86.

On the eight mornings when the wren sang earlier than 5:57½ the light at the time of its first song varied from 0.5 to 1.4 foot-candles, the average being 0.74.

Finally, on the eight mornings when it sang later than 5:58½ the light at the times of its first song also varied from 0.5 to 1.4 foot-candles, but the average was 0.90.

Considering no more than these figures, it would seem that light has little or nothing to do with the time of the first song, for light was, on the average, actually less when the bird sang early than when it sang late. However, Table 1 shows that whenever the bird sang early the light was stronger than normal for that time of day, although five of these eight days were in December, when the sun was rising five minutes later than at the start of the observations. When the bird sang late the light, because of clouds, was less than the average for the time of day. The average deficiency of light at the times of late singing was 0.40 foot-candles and the average excess of light at the times of early singing was 0.43 foot-candles.

Doubtless many other factors than light influenced the time at which this wren started its day but, to give an answer to the problem as stated, the wren seems to be a combination of clock and photometer. Furthermore, the absolute strength of the light seems to be less important than its relative strength as compared with the normal for the time. In other words, the bird strongly tends to start each day at the same time, say 5:58. However, if the morning light be relatively bright, the first song is early and, if the sky be clouded so that the light is relatively weak, the first song is late even though in the first case the light at the time of the first song is really weaker than in the second case.

The light measured by the General Electric foot-candle meter is that which is visible to us. Since there is no evidence that birds can see any light which we can not see, readings on such an instrument are probably sufficient when dealing with such animals, although the possible error introduced by a different distribution of visual intensity within our spectrum should be kept in mind. However, when dealing with insects that, on the one hand, see a large part of our spectrum poorly, if at all, and that, on the other hand, see ultraviolet, which we can not see, such an instrument is not entirely satisfactory.

It is true that the intensity of ultraviolet in sunlight varies roughly as the light visible to us varies; but its intensity, both absolute and relative, is greatly influenced by moisture and other factors. Certain photo-electric cells have sensitivity curves which are similar to the probable sensitivity of insect vision. One such is the Burt cell, and Alfred L. Loomis kindly loaned me a Burt photometer using this cell.

During a former stay at the Barro Colorado laboratory I had be-

	Date	Time of First Song	Observed Light at First Song	Normal Light for that Time	Observed Light Minus Normal
Early	Dec. 5	5:49	0.5	0.156	+0.344
	" 3	5:50	1.4	0.178	+1.222
	" 4 " 2	5:51½ 5:51½	0.6 0.6	0.219	+0.381[1]
	" 1	5:54	0.8	0.301	+0.499
	Nov. 22	5:56	0.8	0.416	+0.384
	" 21	5:56½	0.5	0.469	+0.031
	" 9	5.57	0.7	0.522	+0.178
Late	Nov. 13 " 17 " 20	5:59 5:59 5:59	0.5 1.0 0.7	0.823	—0.090[1]
	" 19 " 23	6:00 6:00	0.5 0.7	1.045	—0.445[1]
	" 26 " 29	6:01 6:01	1.0 1.3	1.350	—0.200[1]
	" 27	6:04	1.4	3.040	—1.640

Table 1.—See Text

come interested in the probability that light was a factor in fixing the time at which leaf-cutting ants started their daily excursions (Lutz, 1929, 'Observations on Leaf-cutting Ants,' Amer. Mus. Novitates, No. 388). I had hoped that the Burt photometer would enable me to test this conclusion and to extend the observations to other species during the present stay. However, the available colony of ants was found to have been unfortunately destroyed and still more unfortunately the moisture of the air, especially in the tropical forest during the rainy season, so interfered with the delicate electrical adjustment of the Burt photometer that the instrument could not be used at that season and place. The

[1]Average.

following short series of observations on a colony of stingless bees (*Trigona mosquito*, probably an undescribed subspecies) were made with the slight help that could be had by the use of the General Electric foot-candle meter measuring the light visible to us but not the insects' range.

A colony of this species of stingless bee had its nest between the inner and outer walls of a cottage near the laboratory. Entrance and exit was through a slit at the edge of the door-frame of the cottage. Over this slit the bees had made a somewhat dome-shaped oval cover, chiefly of wax. This cover was about 1¼ inches in its longest (vertical) diameter. During the day, when the colony was active, there was a definite, circular opening at the lowest part of the cover. When in use, this "portal" was not much larger than necessary for one bee at a time to pass through.

At night the portal was closed by continuing the waxen cover directly across it. But, even then, the lower part of the cover was not entirely solid, there being numerous small "pin-holes" in its substance.

When getting ready for a day's activity the bees did not open the portal directly. There was a realtively long process of biting off wax here and there from the inside of the lower part of the cover and applying it elsewhere. This often resulted in numerous, rather large holes being made and filled, until finally work was concentrated at the place where the portal was to be.

During the last week of November and the first of December, so far as could be seen by looking through the small holes that were in the bottom third of the nest-cover even at night, the bees did not usually start operations on it before about 7:00 A.M. When work did start one could, with difficulty, see one or two bees moving about, but the best evidence of their activity was the occasional protrusion of antennæ through the small holes.

Having in mind that some changing feature of the environment may be the "signal" to the bees that it is time to open the portal I at first thought that these protrusions of the antennæ might be for the purpose of better sensing the environmental factor. However, I finally concluded that the protrusions were quite accidental. The bees, working with their mandibles, had their face against the cover; and the antennæ, being on the front of the head, would quite naturally poke through any opening there might be in the cover against which they were pressed.

What factors of the environment, important enough to have an

influence and variable enough to have their changes noticed by the bees, would reach the bees spending the night under this cover? Both the temperature and the humidity even as late as eight o'clock were not very different from what they had been during the night. In fact, during the two weeks when these factors were measured between early morning and about ten o'clock the entire temperature range was only five degrees (23° to 28° C.) and the range of relative humidity was only eighteen per cent (80 to 98). Light, however, ranged from none to more than 100 foot-candles, the upper limit of the General Electric foot-candle meter. Furthermore, changes in light could easily be perceived by the bees through the small holes in the nest-cover, while it is improbable that small external changes in either temperature or humidity would quickly affect the space under the cover. Accordingly, if any external factor influences the time of opening the nest, there is some reason to suspect that the factor is light.

As it is impossible to determine definitely when work begins on the inside of the cover or even to say definitely when the opening of the portal is completed, since the bees may work on it for some time after it is large enough for a bee to pass through it, I took as the main event to be checked against external factors the first flight of a bee from the nest.

Anyone who has tried constantly watching a small opening for the quick flight of a still smaller insect knows the eye-fatigue and the occasional, spasmodic "going out of focus" that ensues. I do not now think that I missed any first flights, but on a number of mornings I stopped watching when, seeing a bee returning to the nest before I had seen one go out, I thought that I had. This happened so often that I began to get suspicious and finally there was a dramatic demonstration that at least occasionally some members of the colony may spend the night outside of the nest. It was as follows.

A large jumping-spider (attid) had its retreat in a crack about four inches above the *Trigona* nest. This spider usually came out of its retreat and began its watch for prey before the bees opened their house. One dark, rainy morning, when the bees did not start working on the cover until about nine o'clock and at 10:15 had not yet made any holes large enough for a bee to get through, a member of the colony came flying home. As she flew around trying to get in, the spider jumped at her from a distance of about a foot. The spider missed but, as usual, it had spun a silken thread as it went through the air. One end of this thread was, of course, fastened to the place from which the spider

jumped but I was amazed to see that the spider stopped spinning exactly at the place where it missed catching the flying bee and was brought up in midair with a jerk. Swinging like a pendulum back to firm footing, the spider jumped again for the bee, which had then alighted on the still unopened nest cover, and this time the spider did not miss.

Usually the completion of the portal is not immediately followed by a flight from the nest. The ordinary procedure is for a bee to station itself in the doorway, head and thorax out, apparently waiting for something. During this waiting the bee twists its head from side to side in a way that would be comical were it not so provoking to a human who could not rest his own eyes for a moment lest he miss the bee's flight. On one maddening morning this performance was kept up for more than an hour. Occasionally the bee may crawl onto the outside of the cover or even take a flight of a foot or two, only to go back. Such an excursion was not counted as a real flight. When a bee that had spent the night elsewhere returned, the bee waiting to start would let her in and resume the watch.

Is there an object in this waiting and, if so, what is it? I am inclined to think that light is an important factor in determining both the opening of the nest and the first flight from it; but I have not even a guess as to whether this factor is the absolute intensity of the light or, as seemed to be the case with the wren, if it is the light's relative intensity. Furthermore, the following proof of the importance of some feature of the light is not entirely satisfactory, particularly as there is no measure of its ultraviolet component.

Under normal circumstances the nest's portal is not closed until after sunset. I made a cone of black paper and put it over the nest-cover at 1:30 P.M. When examined at 3:10 the nest was closed as is normal during the night. The cone was then removed and when the nest was examined twenty minutes later the portal was open as is normal during the day.

Of nine "first flights" definitely recorded under normal conditions those on November 23, 24, 27, and December 4 were between 9:00 and 9:30; the one on November 29 at 9:48; and those on November 28 and 30 and December 1 and 2 were between 10:30 and 10:45. Were the environmental factors in the four first-mentioned mornings different from those in the four last-mentioned ones? The first were all clear, November 27 and December 4 particularly so. November 28 was cloudy at 7:00 and it rained from 7:30 to 8:00. On November 30 it rained from 7:35 to 8:45 and then continued cloudy. However, the

mornings of December 1 and 2 were fairly clear. There did not seem to be anything in the weather that would account for the late flights on the last two days.

It happened that, so far as I could tell, the mornings of December 3 and 4 were about as nearly alike, one to the other, as two mornings could well be. Both were practically cloudless. This was particularly fortunate because during the morning of December 3 the nest was intentionally shaded with a canopy of black cloth. This canopy did not come within eight inches of the nest at the closest place. It was complete above and at the outer side from which the main light came. The bottom edge of the canopy was six inches below the level of the nest but there was a space of three feet between it and the edge of the porch floor, which was about nine feet above the ground. Accordingly, there was a free circulation of air which assured little alteration of temperature and humidity. So far as the humanly visible light was concerned, the nest was rather effectively shaded. Thus, at 7:45 the meter showed only 1.5 foot-candles at the nest under the canopy although just outside the light was too strong for the meter to measure (i.e., more than 100 foot-candles). However, ultraviolet is not so easily cut off by a screen, especially when there is much moisture in the air. It "goes around the corner." This is the reason that shadows are weak in photographs taken by ultraviolet. Therefore, it is probable that my screen was not as successful in shading the nest from the rays which might affect the bees as it was in its effect on human eyes. On the otherwise apparently similar morning of December 4 there was no canopy.

On the artificially shaded morning the bees began moving about inside at about 7:45 but by 8:30 there was, as yet, no definitely enlarged hole in the nest-cover. By 9:30 the bees had made an irregular opening in the bottom of the nest-cover but during the next fifteen minutes they more or less closed it and enlarged a number of small holes elsewhere. By 10:00, however, there was a fairly well-finished portal and at 10:10 a bee crawled out and walked about on the nest-cover, returning inside without flying. This was repeated several times and meanwhile two bees that had spent the night away from home returned and, without being considerably bothered by the canopy, flew under it and entered the nest. At 10:20 a bee left the nest and flew directly under the edge of the canopy and away.

On the unshaded morning (December 4) the nest-cover was being opened at 7:30. By 8:30 there was a fairly large irregular hole at the bottom of the nest-cover. By 9:00 the portal was completed and at 9:05 a bee came out and flew away.

The impression—and it is really no more than that—which I got from watching these bees is that, as seemed to be the case with the wren, the bees when starting the day's activities are acting as though they are a "combination of an alarm clock and a photometer." The "alarm clock" is a rather mysterious physiological rhythm similar to that with which we are familiar if we tend to awaken at the same time each morning, no matter where we are. The physiological rhythm under discussion here seems to be modified by variations in light. In the case of the bees one may expect the important part of the light to be the ultraviolet and this is further indicated by the greater effect of the afternoon experiment with a small cone than that of the morning canopy just described. The edges of the cone fitted rather closely so that it cut off the ultraviolet about as effectively as it did the humanly visible light. The canopy, on the other hand, being open below and somewhat so on one side, probably admitted a rather high percentage of ultraviolet. The explanation of the unexpected lateness on December 1 and 2 may be that there was something in the atmospheric conditions of those days which made them seem to the bees relatively darker than they seemed to us. At any rate, it would be interesting to have further data along this line.